

THE AMMONITE SUBFAMILY LABECERATINAE SPATH, 1925:
SYSTEMATICS, PHYLOGENY, DIMORPHISM AND DISTRIBUTION
(WITH A DESCRIPTION OF A NEW SPECIES)

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(With 18 figures)

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ABSTRACT

Systematics of the subfamily Labeceratinae Spath, 1925, are discussed. Data from Zululand suggest that the subfamily probably consists of a single, dimorphic genus, to which the names *Labeceras* and *Myloceras* have been applied. Distribution of the subfamily shows concentration in two main areas—southern Africa—Madagascar and Australia. Comparisons of the faunas of these suggest a high degree of endemism, and also show that post-mortem drift is negligible. Absence of labeceratine faunas from the south Atlantic—with the exception of a single locality in the Austral Basin of southern Patagonia—may possibly be linked to the opening of the Atlantic and the associated different environments, but also the differential ecological requirements of the different ammonite taxa, of which we know nothing.

CONTENTS

	PAGE
Introduction	189
Systematics, phylogeny and dimorphism	190
Distribution	200
Biogeographic and stratigraphic implications	204
Description of a new species	211
Acknowledgements	214
References	215

INTRODUCTION

The ammonite subfamily Labeceratinae Spath, 1925, is a small group of heteromorphs, restricted to the Upper Albian, and generally assumed to be south Gondwanid or Austral in distribution (Collignon 1932: 25; Venzo 1936: 124; Collignon 1950: 84; Wiedmann 1965: 443; Kennedy 1972: 402; Förster 1975: 173; 1981: 168; Klinger 1976: 37; McNamara 1978: 240). The size of the group, conspicuous morphology, and short temporal and limited geographical occurrence is ideal for studying some identifiable factors that may have influenced the palaeobiogeographical distribution.

SYSTEMATICS, PHYLOGENY AND DIMORPHISM

Taking Wright's (1957: L231–L232) classification as a starting point, the systematics of the group may be discussed.

Superfamily SCAPHITACEAE Meek, 1876

Family **Labeceratidae** Spath, 1925

(= Aleteceratidae Whitehouse, 1926; Myloceratidae Spath, 1939)

Genus *Labeceras* Spath, 1925

Subgenus *Labeceras* (*Labeceras*) Spath, 1925

Subgenus *Labeceras* (*Appurdiceras*) Whitehouse, 1926

Genus *Myloceras* Spath, 1925

Genus *Ellipsoceras* Collignon, 1950

(= *Abadieceras* Collignon, 1950)

? Genus *Hamitoides* Spath, 1925

This classification was based mainly on ideas of Spath (1925: 191, *et seq.*; 1930: 57; 1939: 600–601), many of which no longer hold true or need updating. The alleged scaphitoid affinity of the subfamily as advocated by Spath (1925: 191; 1939: 601), and followed by Wright (1957: L231) and Luppov & Druschits (1958: 125), was based on superficial homoeomorphy and incorrect interpretation of sutural data. It was questioned by Schindewolf (1961: 109) and convincingly disproved by Wiedmann (1962: 84; 1965: 443) and Wiedmann & Dieni (1968: 74), who would rather place the group in the family Anisoceratidae, a view followed by Reyment (1964*b*: 37), Klinger (1976: 36) and McNamara (1978: 232). But, as Förster (1975: 172) has pointed out, the trifold lobes are more like those of Ancyloceratinae rather than Anisoceratidae with predominantly bifid lobes. However, the stratigraphic gap between the last occurrence of Ancyloceratinae at the top of the Lower Albian, and the first occurrence of Labeceratinae at the base of the Upper Albian has to be bridged.

I previously (Klinger 1976: 41, pl. 12 (figs 3–4, 6), text-figs 7i–j, 8a), recorded *Labeceras* sp. nov. aff. *L. crassicostatum* from the third, possibly fourth, division of the Albian of Zululand. Additional material (Fig. 1) has since been found that suggests the presence of an as yet unnamed heteromorph with labeceratid coiling and simple sharp ribbing, and another with apparent crioceratid coiling and ventrally tuberculate fine ribbing. The sutures have asymmetrically trifold lobes L, U and I. It would be tempting to regard these as the connecting link between the last Ancyloceratinae and the first Labeceratinae, as envisaged by Förster (1975: 172). However, apart from the suture lines, the regular tuberculation, style of ribbing and planispiral coiling are very difficult to reconcile with the first true Labeceratinae in the Upper Albian of Zululand, and I would rather regard them as homoeomorphic, but ancestrally distinct, hamitids or anisoceratids. Similar faunas were described from the Middle Albian of the Samana Range of India by Spath (1930) and are worth reinvestigating.

In Zululand, the first forms definitely identifiable with *Labeceras* and *Myloceras*, *Labeceras crassetuberculatum* Klinger, 1976 (Fig. 2) and *Myloceras*

rotundum Klinger, 1976 (Figs 3C–E, 4), occur in the lower part of the fifth division of the Albian. Next, *Labecerases plasticum* Spath, 1925 (Fig. 3A) *Myloceras serotinum* Spath, 1925 (Figs 5–6), and *M. cornucopia* Spath, 1925, are common. This association is followed by common *Labecerases inflatum* Förster 1975 (= *Labecerases ovale* Klinger, 1976) (Fig. 7B), *L. rectum* Klinger, 1976 (Fig. 3B), and *Myloceras besairiei* Collignon, 1932. Rare elements in the latter association also include *Ellipsoceras expansum* Collignon, 1950. This is slightly oversimplified (cf. Klinger 1976) but several distinct morphological trends can be observed (Fig. 8). These are from oldest to youngest.

Labecerases

1. Decrease in overall size.
2. Lateral lobe (L) changes from asymmetric to symmetrically trifid.
3. Whorl section becomes more compressed.
4. Coiling initially typically labeceratid, with curved shaft and inward-facing aperture. Later forms with straight shaft, aperture parallel to shaft, very similar or identical to *Myloceras*, and can only be distinguished by virtue of the lateral tubercles.
5. Ornament becomes subdued in later forms and umbilical tubercles reduced.

Myloceras

1. Decrease in overall size.
2. Lateral lobe (L) changes from asymmetric to symmetrically trifid.
3. Whorl section becomes more compressed.
4. Coiling on criocone whorls becomes more regular and compact; distinct change in whorl section near point of uncoiling. Shaft possibly tends to recurve in *Ellipsoceras*.
5. Ornament initially very irregular with variable number of minor to major and/or tuberculate to non-tuberculate ribs. Ribbing later more regular and tending to become more uniform.

Given the range of diversity and also overlap of coiling in Labeceratinae, I doubt if *Ellipsoceras* deserves separate generic rank. Apart from the curious coiling, which has so far been observed only in the holotype of *Ellipsoceras expansum* (Collignon, 1950, pl. 14(5) (fig. 2)), *Ellipsoceras* has ornament of the type of *M. besairiei* Collignon, and is here included in the synonymy of *Myloceras*.

Against this background it is now possible to look at the systematic position of the poorly known genus *Hamitoides* Spath, 1925, which had in the past either been referred to the Labeceratinae with doubt (Spath 1925: 191; 1930: 57; 1939: 600; Wright 1957: L232; Klinger 1976: 36–37) or was considered to be a link between *Hamites* and *Labecerases* (Spath 1925: 191; 1939: 601; Haas 1942: 187; Wiedmann 1962: 98; Wiedmann & Dieni 1968: 74).

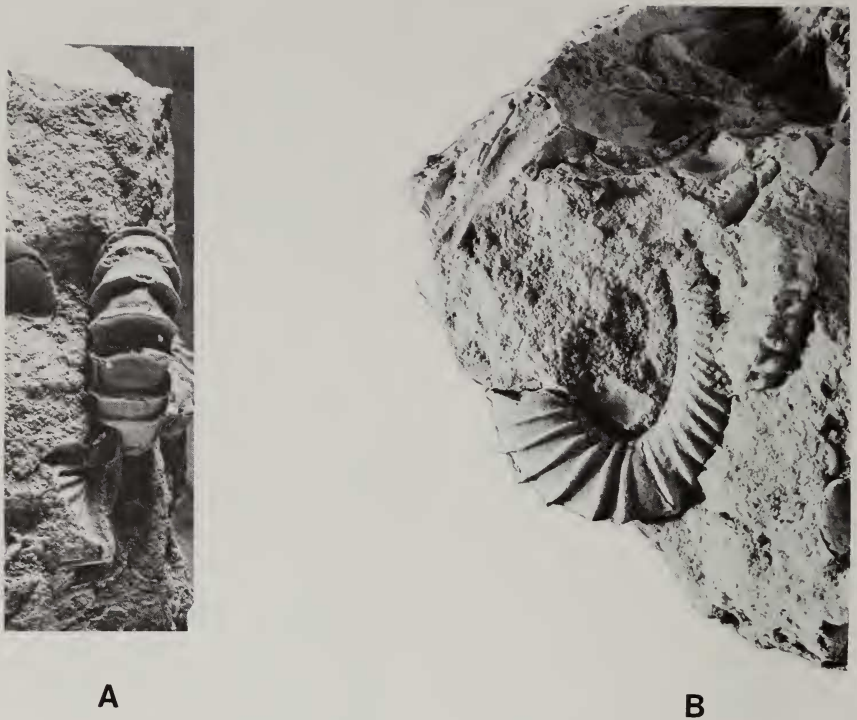


Fig. 1. Gen. et. sp. indet (*Hamites?*), SAM-KK154. Material previously described by Klingler (1976: 41, pl. 12 (figs 3-4, 6), text-figs 7i-j, 8a) as *Labeceras* sp. nov. aff. *L. crassicosatum* from Albian III-IV? Note association with *Lyelliceras lyelli*. $\times 1$.

The type species of *Hamitoides*, *H. studerianus* as interpreted in terms of the lectotype of the species (in Pictet 1847, pl. 15 (fig. 1)), is certainly not a labeceratid. The straight shaft and rounded whorl section are combinations as yet unknown in Labeceratinae, especially in view of the fact that the type material ranges from the Middle Albian to the lower Upper Albian.

Several alleged *Hamitoides* have been recorded from the Middle Albian of Madagascar: *Hamitoides?* *madagascariensis* Breistroffer (1936: 174, pl. 20 (figs 6-9, fig. 10i); Collignon 1963: 45, pl. 258 (figs 114-115)), *Hamites studeri* (Collignon, 1932: 22, pl. 4 (figs 10-13)), *Hamitoides* aff. *studer* (Collignon 1963: 43-45, pl. 257 (figs 1110-1111), pl. 258 (fig. 1116)).

The specimens referred to the type species by Collignon (1963) may, according to Wiedmann & Dieni (1968: 74), possibly belong to *Eoscaphtes tenuicostatus* (Pervinquière) and not involve Labeceratinae at all. *Hamitoides madagascariensis* is too poorly known for definite comment.

Venzo (1936: 111 (53)) recorded two specimens from Zululand as *Hamites studeri*. These are misidentified shafts of *Labeceras plasticum*. *Hamitoides* sp.

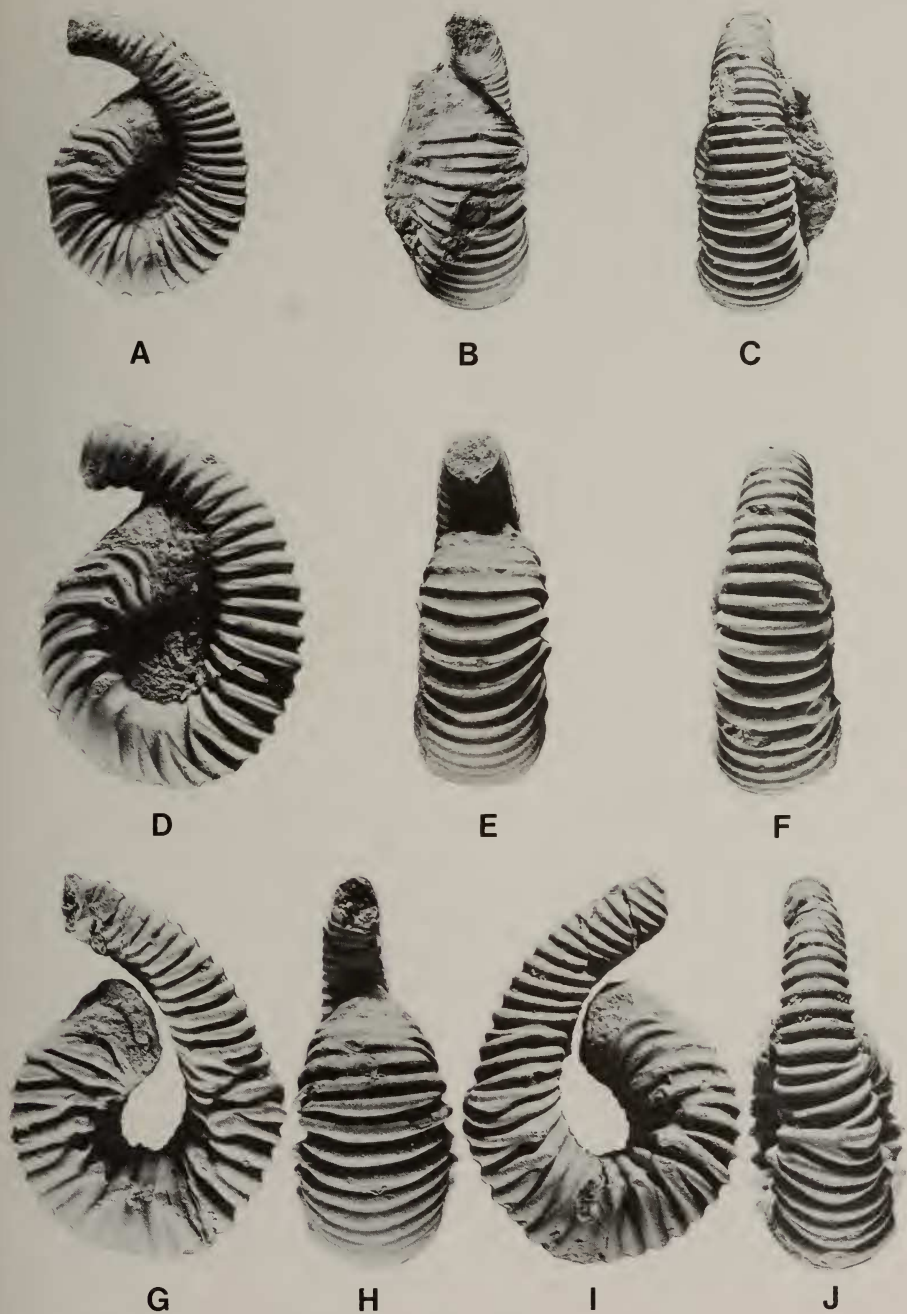


Fig. 2. *Labecerat crassetuberculatum* Klinger, 1976. A-C. NMB-D578.
 D-F. SAM-PCZ205/5/7/, the holotype. G-J. NMB-D2372.
 All $\times 1$.

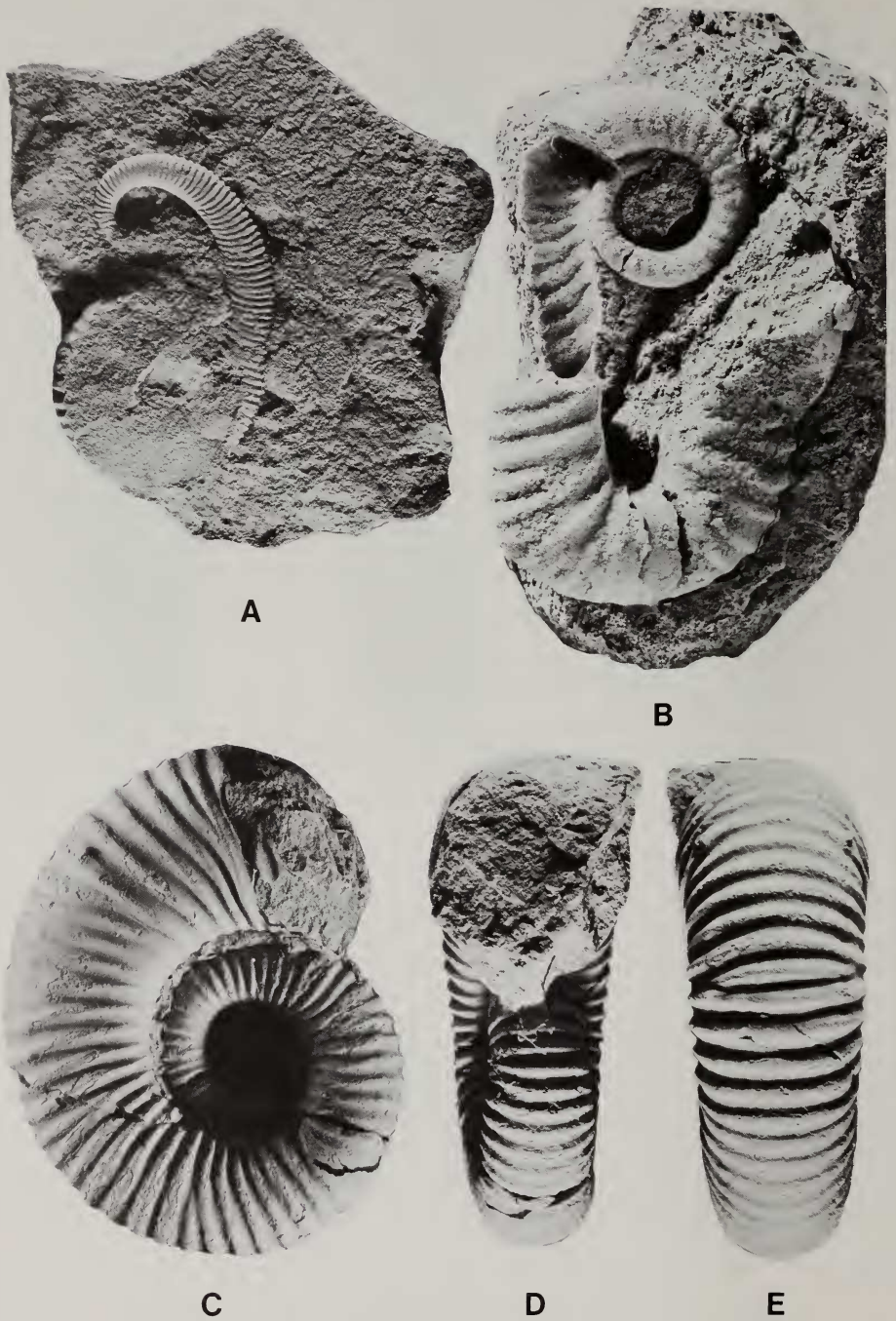


Fig. 3. A. *Labeceras plasticum* Spath, 1925. SAS-EM127. $\times 1$. B. *Labeceras rectum* Klinger, 1976. NMB-D736. $\times 2$. C-E. *Myloceras rotundum* Klinger, 1976. NMB-D496. $\times 1$.

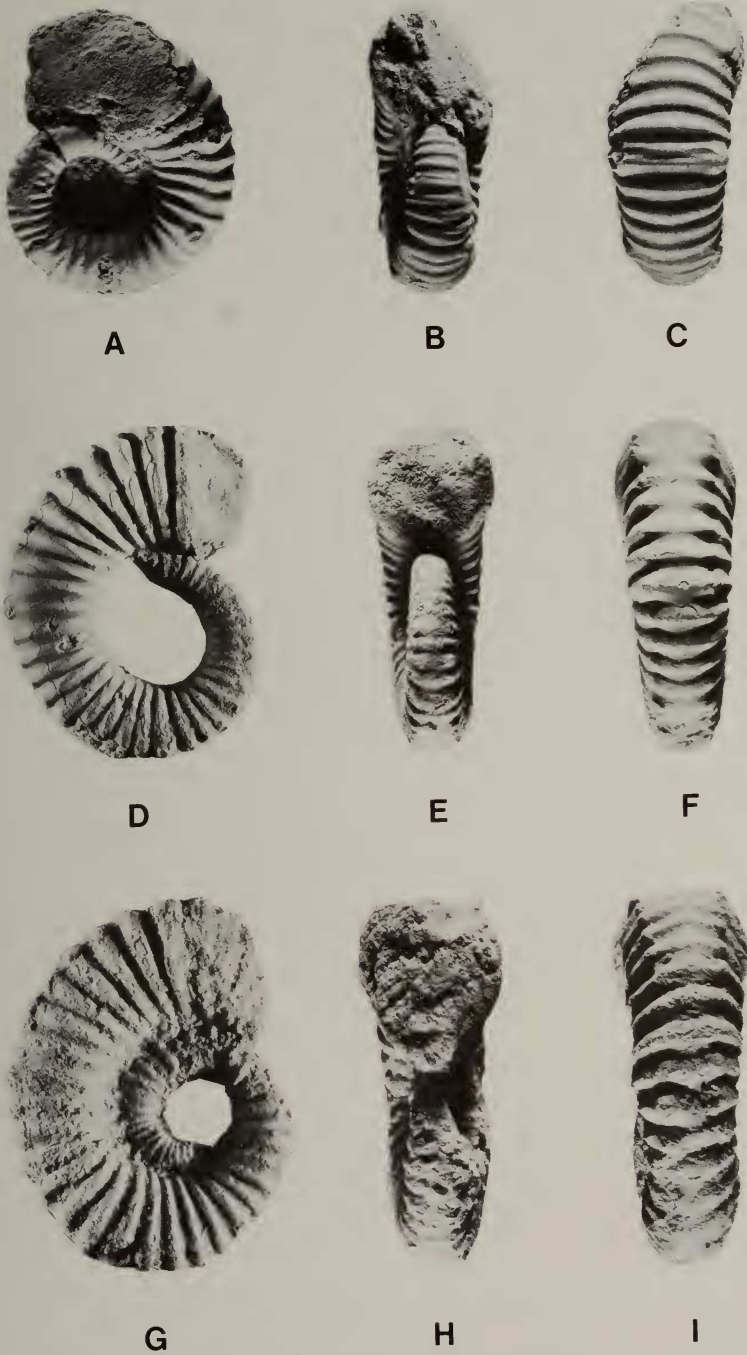


Fig. 4. *Myloceras rotundum* Klinger, 1976. A-C. NMB-D429. D-F. NMB-D294a. G-I. NMB-D294b. All $\times 1$.

ind. from the Samana Range of India (Spath 1930: 62) was neither figured nor described and I cannot comment on it.

Hamitoides angolanus Haas (1942: 187, pl. 45 (fig. 3a–e), text-figs 28a–b) is from the Upper Albian of Hanha, Angola. The holotype consists of a recurved hook and part of the shaft. It is wholly septate, thus definitely excluding labeceratine affinities—rather suggesting ptychoceratid affinities. Thus interpreted, *Hamitoides* definitely does not belong in the Labeceratinae.

McNamara (1980: 147) has recently shown that the type species of *Labeceras* (*Appurdiceras*) Whitehouse, 1926—*Ancyloceras corcyepoides* Etheridge (1905: 14, pl. 1 (figs 3–5), pl. 2 (fig. 4)), is in fact an anisoceratid and should be removed from Labeceratinae. The subfamily Labeceratinae is thus effectively reduced to the two genera, *Labeceras* and *Myloceras*.

Below generic rank, systematics of the Labeceratinae becomes difficult, due to the low specific diversity but extreme intraspecific variation. However, one of the most consistent features of labeceratid systematics is the consistent association of *Labeceras* and *Myloceras* (e.g. McNamara 1978: 241) throughout the known stratigraphic range of the group.

Distinct successive pairs of *Labeceras* and *Myloceras* can be recognized. In both there seems to be an increasing trend towards hydrodynamic stability and/or 'streamlining' of ornament. This leads to surprising homoeomorphy between *Labeceras* and *Myloceras* (Fig. 7).

This raises the question of dimorphism in Labeceratinae—i.e. whether *Myloceras* is the macroconch and *Labeceras* the microconch.

Apart from the scaphitids (see e.g. Makowski 1963; Cobban 1969), dimorphism has only recently been recognized in heteromorph ammonites and remains largely to be explored in Cretaceous groups (see Callomon 1981: 267).

Distinct dimorphism has been recognized in the baculitid genera *Sciponoceras* (Marcinowski 1980: 253; see also Kennedy & Juignet 1983: 17), *Lechites* (Cooper & Kennedy 1977), *Baculites* (Kennedy 1984: 143—in *Baculites incurvatus*; Klinger & Kennedy in prep.—in *Baculites capensis*), and in the heteroceratine species *Colchidites vulanensis* (Aguirre Urreta & Klinger 1986: 350). It has also been suggested for several other groups, e.g. *Bostrychoceras* (Kennedy 1986: 95), *Eubostrychoceras* (Kennedy 1986: 101), *Hamites* (Cooper, unpublished data; Kennedy & Juignet 1983: 12), *Tridenticeras* (Kennedy 1984: 138), and '*Neancyloceras*' (Klinger 1982: 229).

In most of these groups, dimorphism manifests itself mainly by differences in size and, where preserved, in apertural modifications. This would correspond more or less to Type II dimorphism of Houša (1965), where the sexes differ not only in size, but where the male has apertural outgrowths, such as lateral lappets or a ventral rostrum.

Dimorphism has previously been suggested for Labeceratinae but, in my opinion, for the wrong reasons. Spath (1925: 192) suggested that forms with and those without croziers (in *Myloceras*) might be dimorphs. This would be a situation analogous to that found in *Macroscephites* and *Costidiscus*, as suggested by

**A**

Fig. 5. *Myloceras serotinum* Spath, 1925. SAS-Z174. $\times 1$.

Callomon (1981: 267). However, the Zululand material does not support this view.

Förster (1975: 176) suggested that *L. plasticum crassum*, which consists of predominantly large, inflated, strongly tuberculate forms, may differ from the generally smaller and more weakly tuberculate *L. plasticum plasticum* on account of sexual dimorphism. By analogy with the scaphitids (e.g. Makowski 1963: 31, *et seq.*; Cobban 1969), this is the situation one would expect in *Labeceras*. Also, by analogy with the scaphitids, we would expect the range in size to



Fig. 6. *Myloceras serotinum* Spath, 1925. A-B. SAS-Z174. $\times 1$.

be such that the largest microconchs would be larger than the smallest macroconch, but not as large as the largest macroconch. In the available material we find that the coarsely ornamented forms are generally larger than the more finely ornamented forms, but that the size overlap of these forms is virtually 1:1. Size distribution patterns of *L. crassetuberculatum*, *L. plasticum*, *L. rectum* and *Myloceras serotinum* are shown in Figure 9. Apertural lappets are generally taken to be characteristic of micromorphs. Spath (1925: 192, pl. 31 (fig. 4b-c)) noticed that in *Labeceras plasticum* "The aperture is provided with a short dorsal



Fig. 7. A. *Myloceras serotinum* Spath, 1925. SAM-PCZ7665. B. *Labeceras inflatum* Förster, 1975. NMB-D2702. Both $\times 1$. Note homoeomorphy between *Labeceras* and *Myloceras* suggesting dimorphism.

and two longer lateral lappets' and in *Myloceras serotinum* (1925: 193, pl. 33 (fig. 1)) 'The aperture, as restored . . . shows a slight ventral and two more prominent lateral lappets'. Subsequently Wright (1953: 473) noted that '. . . *Labeceras* has lateral lappets, whereas the probably closely related *Myloceras* has an aperture merely with a sinuous border'.

Material from Zululand shows that lateral lappets occur in both *Labeceras* and *Myloceras* but, that in relation to overall shell size, those of *Labeceras* are much larger than those of *Myloceras* (Figs 13–15).

Thus, unless we are dealing with isochronous parallelism or homoeomorphy, it seems plausible to regard *Labecer* and *Mylocer* as a dimorphic pair—the former being the microconch, the latter the macroconch.

I admit that this may appear as an extreme form of dimorphism not previously recorded in other heteromorph groups. It would be ideal to show that the nuclei of *Labecer* and *Mylocer* are identical, thus lending further credibility to the assumption that they are dimorphs. Unfortunately nuclei are not available and, at the smallest diameters preserved, *Mylocer* is distinctly tuberculate and *Labecer* non-tuberculate. However, if they are indeed dimorphs, the comparisons proposed by Förster (1975: 172–173) between *Mylocer* and *Australicer*, and *Labecer* and *Toxoceratoides*, may not be as preposterous as they seem—although the taxonomic implications are frightening.

This systematic arrangement of the subfamily Labeceratinae seems far removed from that adopted by Wright (1957: L231–L232) but, in the light of current data and from a phylogenetic point of view, makes much more sense. This effectively reduces the subfamily Labeceratinae to one dimorphic genus. Until details of the complex synonymies have been worked out, I prefer to retain both generic names *Labecer* and *Mylocer* in this discussion, albeit mainly for the sake of taxonomic 'neatness'.

Within this systematic framework it is now possible to look at the stratigraphic and geographic distribution of the subfamily Labeceratinae.

DISTRIBUTION

Records of *Labecer* from the Albian of England (Owen 1971: 195) are based on misidentifications of a labeceratid homoeomorph, *Idiohamites ellipticoides* Spath, 1939 (see Kennedy 1972: 400–404). All other records of Labeceratinae are of Gondwanid origin (Fig. 10). These include:

1. *Australia*. Occurrences here are in the Great Artesian Basin of Queensland and in South Australia (see Ludbrook 1966 for summary). Individual references include McCoy (1867), Etheridge (1909—South Central Queensland), Whitehouse (1926—South Central Queensland), Reyment (1964*a*, 1964*b*—South Australia), and McNamara (1978—Central Queensland).

Precise data are not available, but the *Mylocer*–*Labecer* assemblages have been dated as middle Late Albian (McNamara 1978: 231), or as being equivalent to the *varicosum*–*aequatoriale* subzones of the Gault of England (Spath 1925: 194) or possibly the *orbigny* subzone (Whitehouse 1926: 197; also Reyment 1964*a*: 34).

2. *New Guinea*. Glaessner (1958: 217–218) recorded *Mylocer davidi* Whitehouse, *Mylocer* cf. *flindersi* (McCoy), and *Labecer trifidum* Whitehouse from the Albian of New Guinea.

3. *New Zealand?* Wellman (1959: 121) and Henderson (1973: 99) recorded a single questionable fragment of *Mylocer* from the Clarence Series at Wairarapa on North Island.

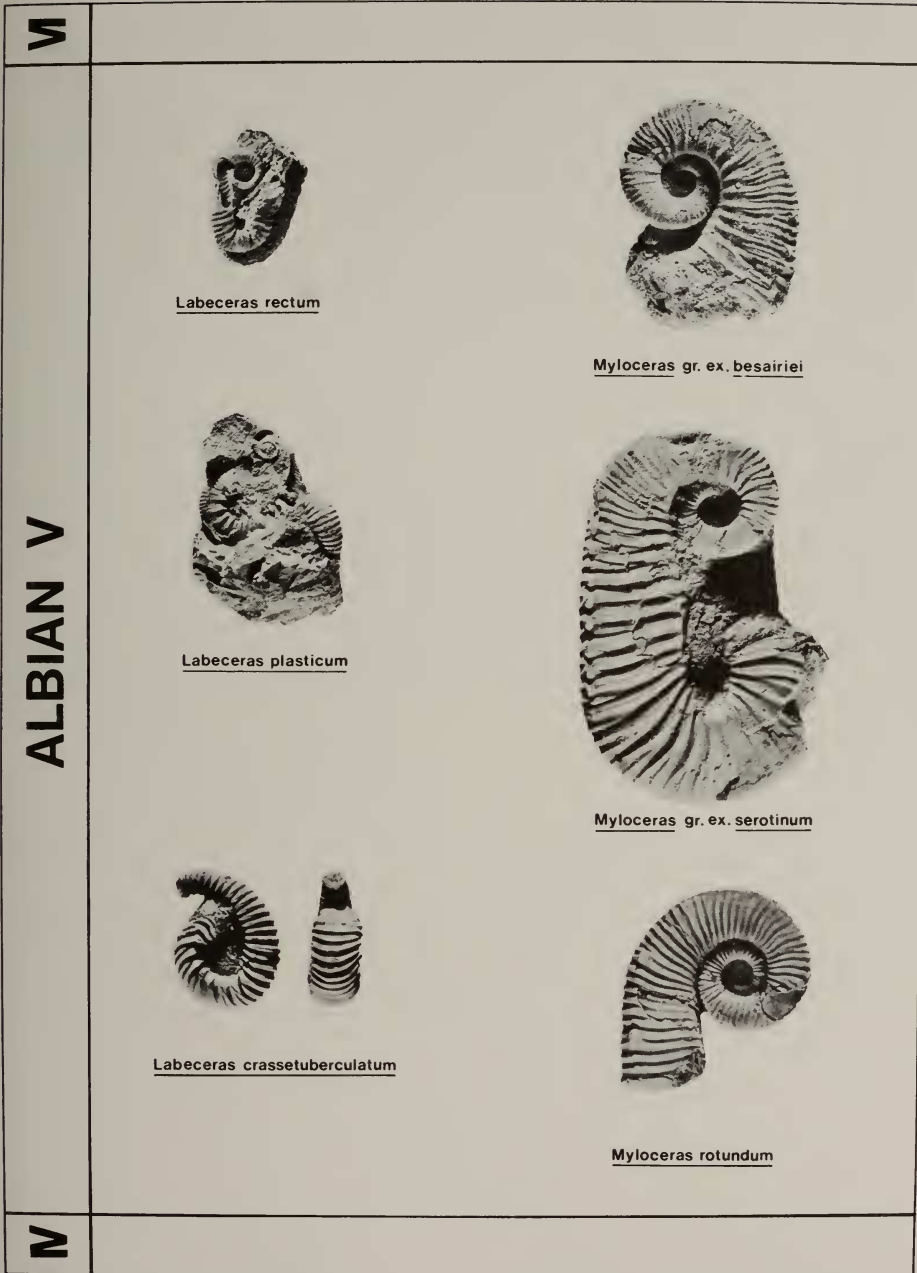


Fig. 8. Suggested phylogenetic sequence of *Labeceras* and *Myloceras* in Zululand. All reduced by various fractions to fit diagram.

4. *Antarctica?* Thomson (1984: 89) mentioned small heteromorphs 'possibly *Labecerases*' from the Albian of Lost Valley on James Ross Island in Lesser Antarctica.

5. *Somalia?* Tavani (1942: 30 (116), pl. 3 (pl. 12) (fig. 8)) recorded a single specimen from the Albian of Sceec Gure (Bugda Acable), Somalia, as *Labecerases plasticum*. The specimen is very poorly preserved but the presence of straight, near-parallel shafts seems to indicate '*Hamitoides*' rather than *Labecerases plasticum* affinities.

6. *Madagascar.* A very well-documented labeceratine fauna is known from Madagascar. Individual references include Boule *et al.* (1907—Andrakaka, Diego-Suarez), Besairié (1932), Collignon (1932—Mont Raynaud), Collignon (1936—Maniamba-amba), Collignon (1950—Mokaraha), Collignon (1951—Andranofotsy, Manja), Collignon (1963—Diego-Suarez, Betioky (Vohimaranitra), Andronofotsy (Manja), Mokaraha (Soalala)), and Besairié & Collignon (1972).

This fauna is well dated and, according to the biozonation compiled for Madagascar by Collignon (1963), ranges from the lowermost zone of the Upper Albian, Zone à *Dipoloceras cristatum*, through the Zone à *Hysterocheras binum* to the penultimate Zone à *Pervinquieria inflata*.

The systematic position of *Euhemihoplites paradoxus* Collignon (1964: 38, pl. 326 (fig. 1457)), reported from the Lower Cenomanian, Zone à *Mantellicerases mantelli* et *Calycoceras newboldi*, should be mentioned here. According to

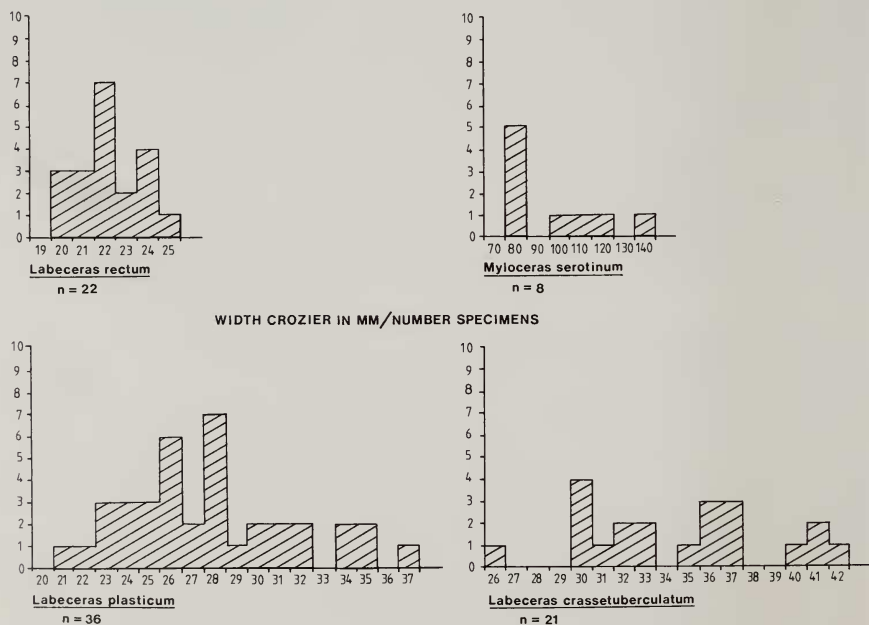


Fig. 9. Size distribution in *Labecerases* and *Myloceras*.

Kennedy (1985), this species, based on a single fragment, may in fact be a *Myloceras*, probably derived from Upper Albian strata. It is similar to a new species described below in possessing umbilical tubercles.

7. *Mozambique*. The original labeceratid material on which Spath's (1925: 191, *et seq.*) descriptions were based, are probably from near Catuane in southern Mozambique—Förster's (1975: 32) locality Lagoa Catuine. Other localities yielding labeceratids include Rio Zepundune, Road Metal Quarry 9,5 km north of Catuane, Rio Comane, and Rio Changalane.

The stratigraphic range of labeceratids in southern Mozambique was compared to the standard European succession of *varicosum* to *aequatoriale* subzones of the *Mortoniceras inflatum* Zone.

8. *Zululand*. Labeceratids are locally very common in Kennedy & Klinger's (1975: 276) fifth division of the Albian. References include Besairié (1930: 622—Mzinene), Venzo (1936: 113 (55), *et seq.*—Ndabana-Mzinene), Kennedy & Klinger (1975: 276), Klinger (1976: 36, *et seq.*—Mzinene River, Ndambana Creek, Ndumu, Mkuze Game Reserve, Munywana River), and Haughton (1936: 292—Pongola River).

Definite *Labeceras* and *Myloceras* first occur in the fifth division of the Albian in association with *Dipoloceras cristatum*, '*Deiradoceras*', '*Drepanoceras*' and '*Rhytidoceras*'. Later forms of the group *Myloceras besairiei*, with extremely compressed whorl section and regular ornament, and *Labeceras rectum* occur in association with *Pervinquieria* (*P.*) and *P.* (*Styphloceras*). In comparison with

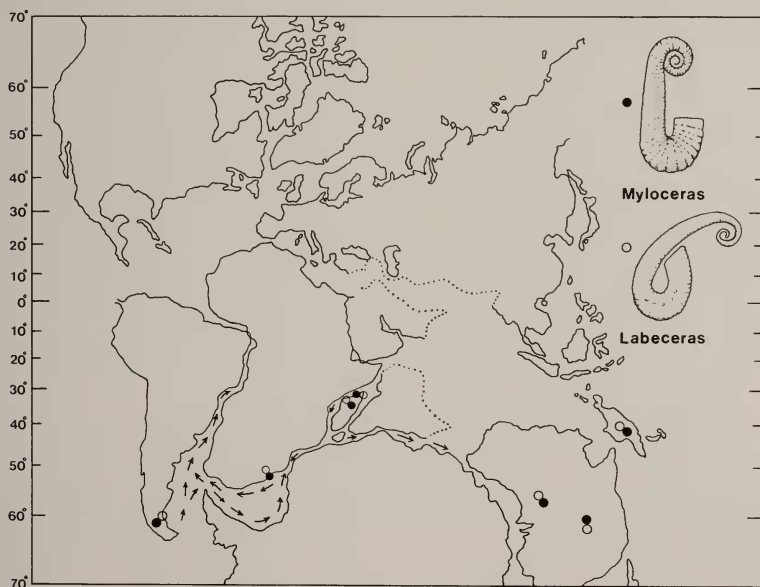


Fig. 10. Palaeobiogeographic distribution of *Labeceras* and *Myloceras*. Map based after Smith & Briden (1973).

Madagascar, this would suggest a definite range of Upper Albian, Zone à *Dipoloceras cristatum* to Zone à *Pervinquieria inflata*.

9. *Argentina* (Patagonia). Leanza (1970: 202, 209) recorded two new genera, *Calliscaphites*, type species *Calliscaphites andinus* Leanza, 1970, and *Paraleptoceras*, type species *Paraleptoceras singulare* Leanza, 1970, from the Albian of Estancia La Vega, in the Santa Cruz Province of Patagonia. These are clearly synonyms of *Myloceras* Spath and *Labeceras* Spath and, from the limited figured material available, seem close to *Myloceras rotundum* Klinger and *Labeceras crassetuberculatum* Klinger.*

Subsequent reports from the Santa Cruz Province include Nullo *et al.* (1981, pl. 2 (fig. 10—*Labeceras?* sp., fig. 11—*Calliscaphites andinus*)) and Riccardi & Rollieri (1980: 1198).

Medina & Rinaldi (1986) recorded both *Myloceras* and *Labeceras* from Estancia La Vega in Santa Cruz Province, as do Riccardi *et al.* 1988. Unfortunately, this is the only known locality in the Austral Basin with labeceratids and, in addition, the outcrop is rather small.

BIOGEOGRAPHIC AND STRATIGRAPHIC IMPLICATIONS

Distribution of the Labeceratinae is strictly Gondwanid—more specifically south Gondwanid. Two features are conspicuous:

1. Concentration of Labeceratinae into two main regions—south-eastern Africa–Madagascar and Australia.
2. Conspicuous absence of Labeceratinae in India and, with the exception of the Austral Basin of Patagonia, absence in the South Atlantic.

South-eastern Africa–Madagascar and Australia

Correlation of Labeceratinae faunas between south-eastern Africa–Madagascar and Australia is tenuous, mainly due to a combination of taphonomy, differential preservation and systematics. Complete specimens of *Myloceras* and *Labeceras* are rare, and most descriptions are based on incomplete material.

To this must be added the effects of disparate sizes and intraspecific variation. Some of the Australian species of *Myloceras* are gigantic, e.g. *Myloceras axonoides* (Etheridge, 1909, pl. 44 (fig. 2)) and *Myloceras nautiloides* (Etheridge, 1909, pl. 45), and no Afro–Malagassy specimens are known that even approximate the Australian giants in size (Figs 11–12).

It is difficult to evaluate the reports of species common to both areas (e.g. Venzo 1936: 55 (113); Reyment 1964a: 23; Förster 1975: 176; Klinger 1976). From these records it appears that the only species probably common to south-eastern Africa–Madagascar and Australia, are *Labeceras bryani* Whitehouse and *L. plasticum* Spath.

Out of a total of about 40 described species, this is indeed a very low correlation factor. However, even given the effects of intraspecific variation, analysis of the faunas still shows some differences.

* See p. 219 for note added at proof stage.

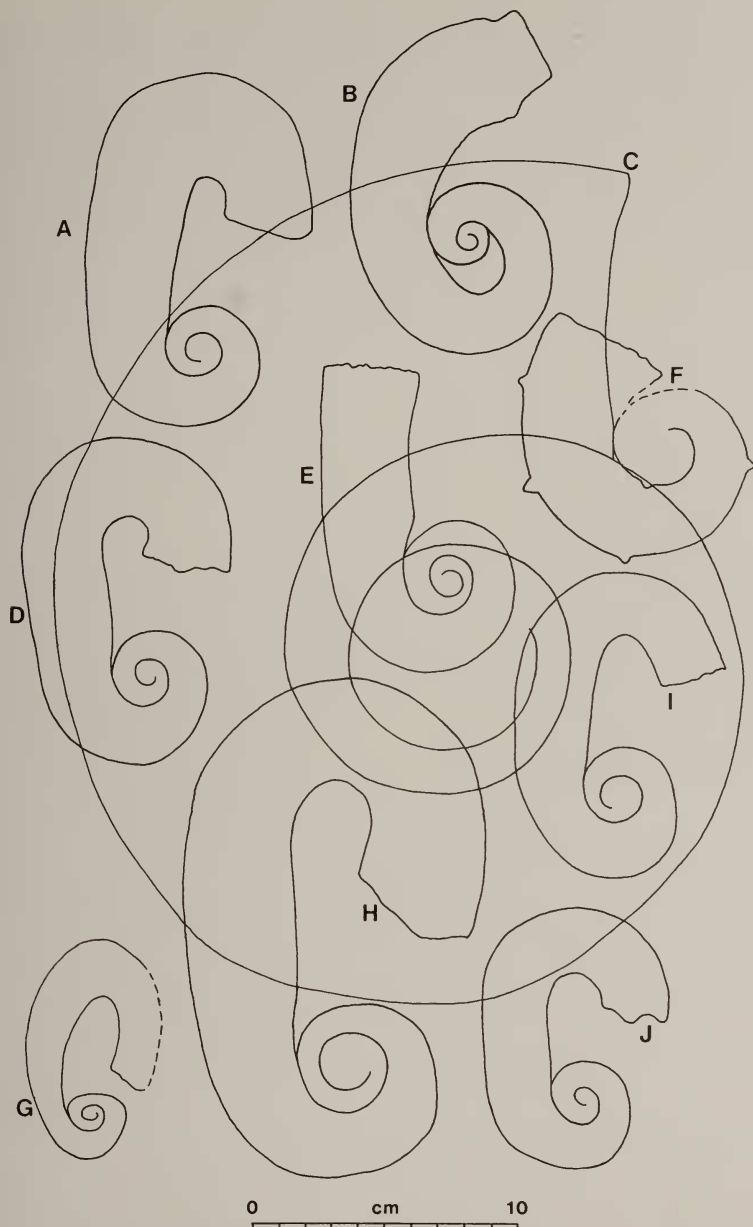


Fig. 11. Variation in size in *Myloceras*. A. *Myloceras serotinum* Spath, 1925. SAS-Z174. B. '*Ellipsoceras*' *expansum* Collignon, 1950. Holotype. C. *M. axonoides* Etheridge, 1909. Holotype. Half size compared to other specimens. D. *M. serotinum* Spath, 1925. SAM-7665. E. *M. cornucopia* Spath, 1925. Holotype. F. *M. amaltheia* Spath, 1925. Holotype. G. *M. mokaharensis* Collignon, 1964. Holotype. H. *M. auritulum* McNamara, 1978. Holotype. I. *M. serotinum rugosa* Spath, 1925. Holotype. J. *M. serotinum* Spath, 1925.

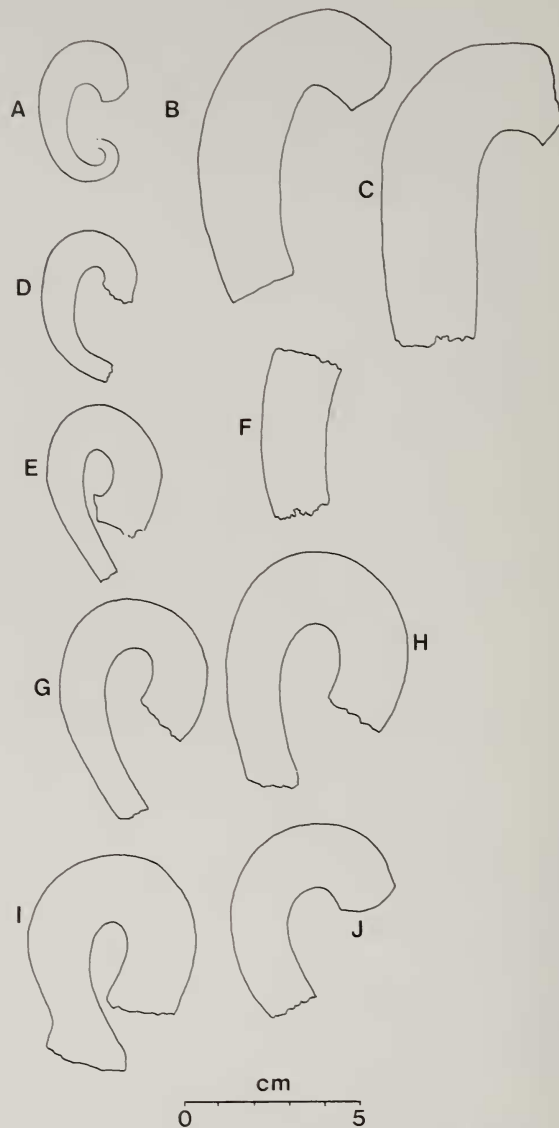


Fig. 12. Variation in size in *Labecerases* (and one specimen of *Myloceras*). A. *L. plasticum* Spath, 1925, the holotype. B. *L. gracilis* Collignon (1964, fig. 1140). C. *Myloceras serotinum elliptica* Collignon (1965, fig. 1137). D. *L. plasticum crassa* Spath, 1925, the holotype. E. *L. etheridgei* Whitehouse, 1926 (pl. 38 (fig. 2)). F. *L. plasticum* (Collignon, 1964, fig. 1125). G. *L. papulatum* Whitehouse (1926, pl. 39 (fig. 3)). H. *L. hourcqii* Collignon (1950, pl. 14 (fig. 1)). I. *L. compressum* Whitehouse, 1926 (1950, pl. 39 (fig. 5)). J. *L. crassicosatum* Collignon, 1950 (pl. 13 (fig. 5)).

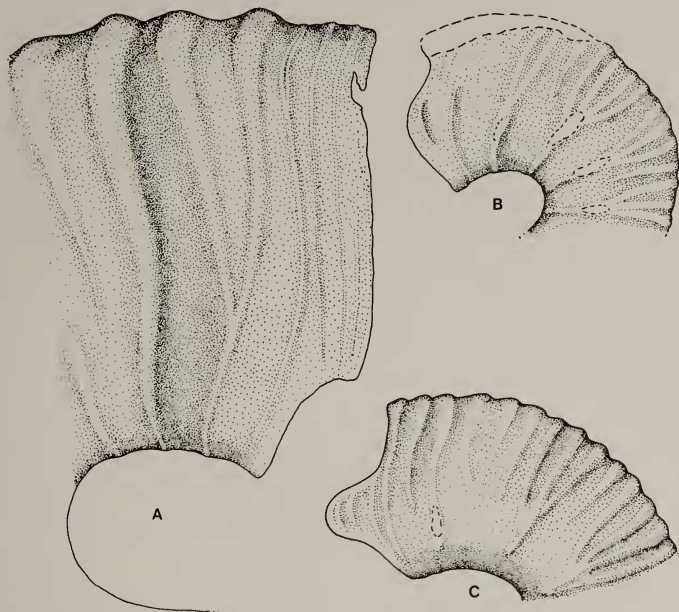


Fig. 13. A. Sketch of aperture of *Myloceras serotinum*. SAM-7665. $\times 3.9$.
B-C. *Labeceras plasticum*. B. SAM-Z450. C. A2173.

The only reliable feature in the systematics of *Myloceras* appears to be the whorl section (see also Reyment 1964a: 31). Taking the phylogenetic sequence (Fig. 8) as a basis for comparison, three groups can be recognized: *Myloceras* gr. ex. *rotundum* with round to reniform whorl section, *Myloceras* gr. ex. *serotinum* with rectangular depressed to compressed whorl section, and *Myloceras* gr. ex. *besairiei* with rectangular to very compressed whorl section. A similar crude analysis can be done on *Labeceras*, based on the nature of the shaft—*Labeceras* gr. ex. *crassetuberculatum* with incurved, asymmetrically coiled shaft, *Labeceras* gr. ex. *plasticum* with distinctly curved shaft, and *Labeceras* gr. ex. *rectum* with straight shaft and very often a distinct nick-point and coiling, virtually as in *Myloceras*.

Within this crude framework Australian and Afro-Malagassy forms can be compared. No forms similar to *Myloceras* gr. ex. *besairiei* or *Labeceras* gr. ex. *rectum* are known from Australia, i.e. comparisons are possible amongst stratigraphic early forms but not amongst the later, established ones.

Though fully aware of the possible errors in the systematics of the subfamily, the above data do point to significant differences between the Australian and Afro-Malagassy faunas, and seem to suggest considerable endemism in the two labeceratine populations, especially as far as the apparent phylogenetically more advanced forms are concerned. This also implies restricted necroplanktonic

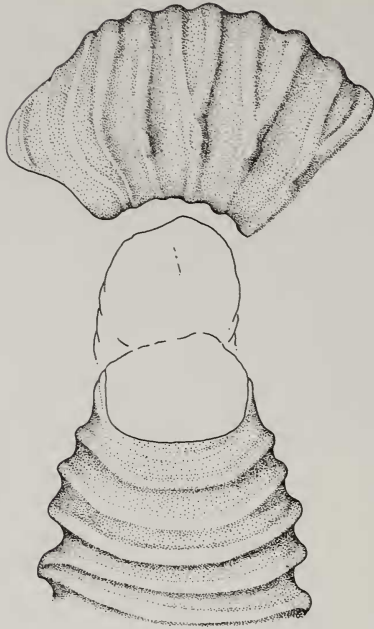


Fig. 14. Sketch of aperture of *Labeceratium crassetuberculatum*. EM 151. $\times 3,9$.

dispersal in at least part of the population, which is at variance with the views held by Reyment (1964a: 33).

India

Data on the Cretaceous of southern India mainly date back to Forbes (1846), Stoliczka (1863–1865), and Kossmat (1895–1898). The most recent stratigraphic syntheses of the Cretaceous of southern India are by Sastry *et al.* (1968) and Gupta (1975). The lowermost Utatur Group is a mixture of Upper Albian and Cenomanian. The lower *Schloenbachia inflata* Zone contains a mixture of Upper Albian and Lower Cenomanian faunas. According to Spath (1925: 196) the sequence only starts with the *aequatoriale* subzone, i.e. the uppermost part of the European *inflatum* zone. Thus, on stratigraphic data alone, chances of finding Labeceratinae in southern India are very slender. New collections being studied by Dr M. A. Ghare (letter 17.7.84) contain numerous new records of heteromorph genera, but no labeceratines.

South Atlantic

Apart from one locality, Estancia La Vega, in the Austral Basin of southern Patagonia, no Labeceratinae are known from the South Atlantic.

The stratigraphic range of the Labeceratinae coincides with part of the opening-up of the South Atlantic Ocean. For discussions see e.g. Beurlen

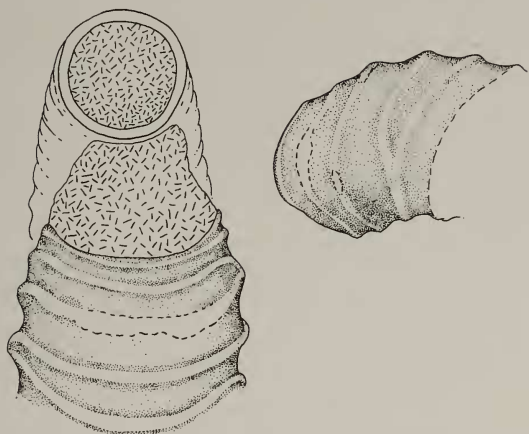


Fig. 15. Sketch of aperture of *Labecerat crassetuberculatum*.
H207/5/7. $\times 3.9$.

(1961), Reyment & Tait (1972), Van Andel *et al.* (1977), Sclater *et al.* (1977), Melguen *et al.* (1979), Reyment (1980), Rand & Mabesoone (1983), etc. It is possible that the distribution of the group may have been influenced in part by these circumstances (Fig. 16).

Whatever the exact dates of North and South Atlantic marine connections may be, it seems reasonable to accept that surface currents existed (Berggren & Hollister 1974; Lloyd 1982) and that free faunal migration was possible between south-eastern Africa–Madagascar, via the Cape Sea Route, through the Atlantic, as far north as the Venezuelan Andes, Mexico and Texas during the Upper Albian (e.g. Kennedy & Cooper 1975: 284–285; Kennedy & Cobban 1976: 77; Förster 1978: 158; 1981: 167–168; Renz 1981: 201; 1982).

Absence of records of Labeceratinae from the Cape Basin is due to the absence of onshore exposures. No onshore Albian exposures are known between southern Angola and Zululand, a distance of some 3 500 km. Offshore drilling on the Orange River delta may hold some prospects. However, the absence of Labeceratinae from the Upper Albian of the Brazil–Angola Basin seems real, and not due to collecting failure, non-exposure of relevant strata or misidentifications, as various extensive faunal lists from this region seem to substantiate, e.g. Spath (1922), Haas (1942), Howarth (1965), Reyment (1955, 1956, 1978, 1981), Cooper (1978), Collignon (1978), and Cooper & Kennedy (1979).

Prevailing conditions in the Upper Albian in the Brazil–Angola Basin seem to have been favourable for development of endemic faunas, e.g. the mortoniceratine genus *Elobiceras* (e.g. Reyment 1981: 149), but unfavourable for the entry of others, e.g. the Labeceratinae, while apparently having no effect on others.

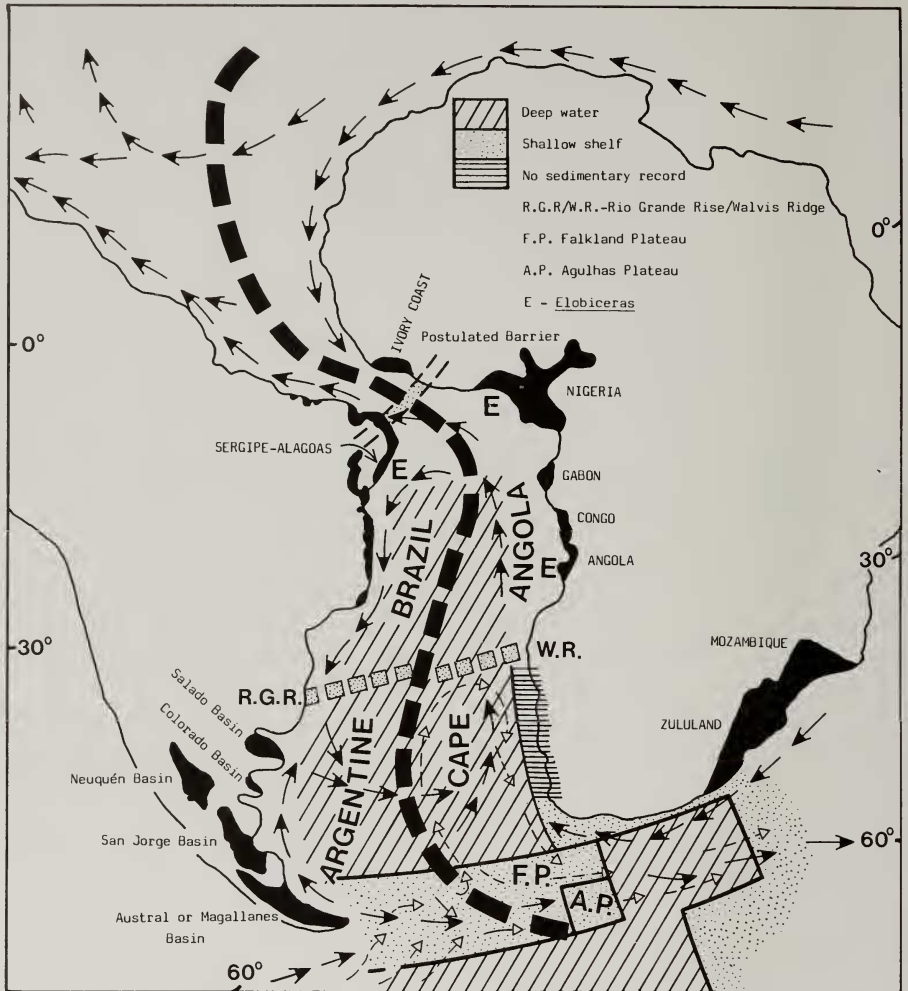


Fig. 16. Palaeo-reconstruction of opening of the Atlantic Ocean. Map based mainly on Dingle *et al.* 1983.

There seems to be little consensus on the physical size and effect of the Walvis Ridge separating the Angola Basin from the Cape Basin, ranging from a submerged chain to a series of islands (e.g. various references in Sclater *et al.* 1977; Bolli *et al.* 1978; Reymont 1980; Rage 1981), nor on its effects on the distribution of invertebrate faunas (e.g. Scheibnerová 1978, 1981; Tambareau 1982; Dingle 1984). However, as the South Atlantic progressively opened, circulation in the Cape Basin seems to have kept one step ahead of that of the Angola Basin, especially after the Falkland Plateau had cleared the tip of Africa at about 100 Ma.

In addition, climatic effects have to be taken into consideration. Plant material from DSDP site 361 suggests a temperate climate and well-vegetated onshore environment off the Cape Basin (although this is questioned by McLachlan & Pieterse (1978), who suggest a harsh, probably dry climate), whereas in Angola the climate was probably warm and arid to semi-arid (e.g. Siesser 1978: 970; Natland 1978; Melguen 1978). Apart from differences in water temperature and also probably salinity and density, these climatic differences are clearly reflected by the different dominant sedimentary facies in the two basins—that of the Cape Basin being predominantly terrigenous (reflecting active erosion and transport by river systems), whereas that of the Angola Basin is more calcareous and pelagic, in accordance with arid climate and low sediment supply. This in turn may be related to differential nutritional resources in the basins.

To summarize, it would seem simplistic to seek a single cause for the lack of Labeceratinae in the eastern South Atlantic. Prevailing surface currents may have been adequate to assist migration of the Labeceratinae into the Atlantic, but a combination of factors, including physical and chemical differences in the Argentine–Cape and the Brazil–Angola Basins, separated by the aseismic Rio Grande Rise and Walvis Ridge, may have acted selectively in producing this palaeobiogeographical distribution pattern. To these must be added the prime, albeit virtually unknown, factors of differential ecological requirements of the different ammonite taxa, which probably completely overshadow all the other restricting factors.

DESCRIPTION OF A NEW SPECIES

Myloceras bituberculatum sp. nov.

Figs 17–18

Type

Holotype is SAM-PCZ7299a (ex Van Hoepen Collection, uncatalogued specimen); probably from the lower reaches of the Mzinene River, Zululand, Mzinene Formation, Upper Albian.

Material

Paratypes are SAM-PCZ7299b, PCZ7300–7304, PCZ8331–8338 (ex Van Hoepen Collection, uncatalogued specimens); probably all from the lower reaches of the Mzinene River, Zululand, Mzinene Formation, Upper Albian.

Description

The material consists of crioceratitid phragmocones only; the uncoiled section is unknown. Coiling is relatively tight for *Myloceras*, with successive whorls just touching, and the ventral ribs and tubercles of the preceding whorls slightly impressed in the dorsum of succeeding whorls. Umbilical width increases

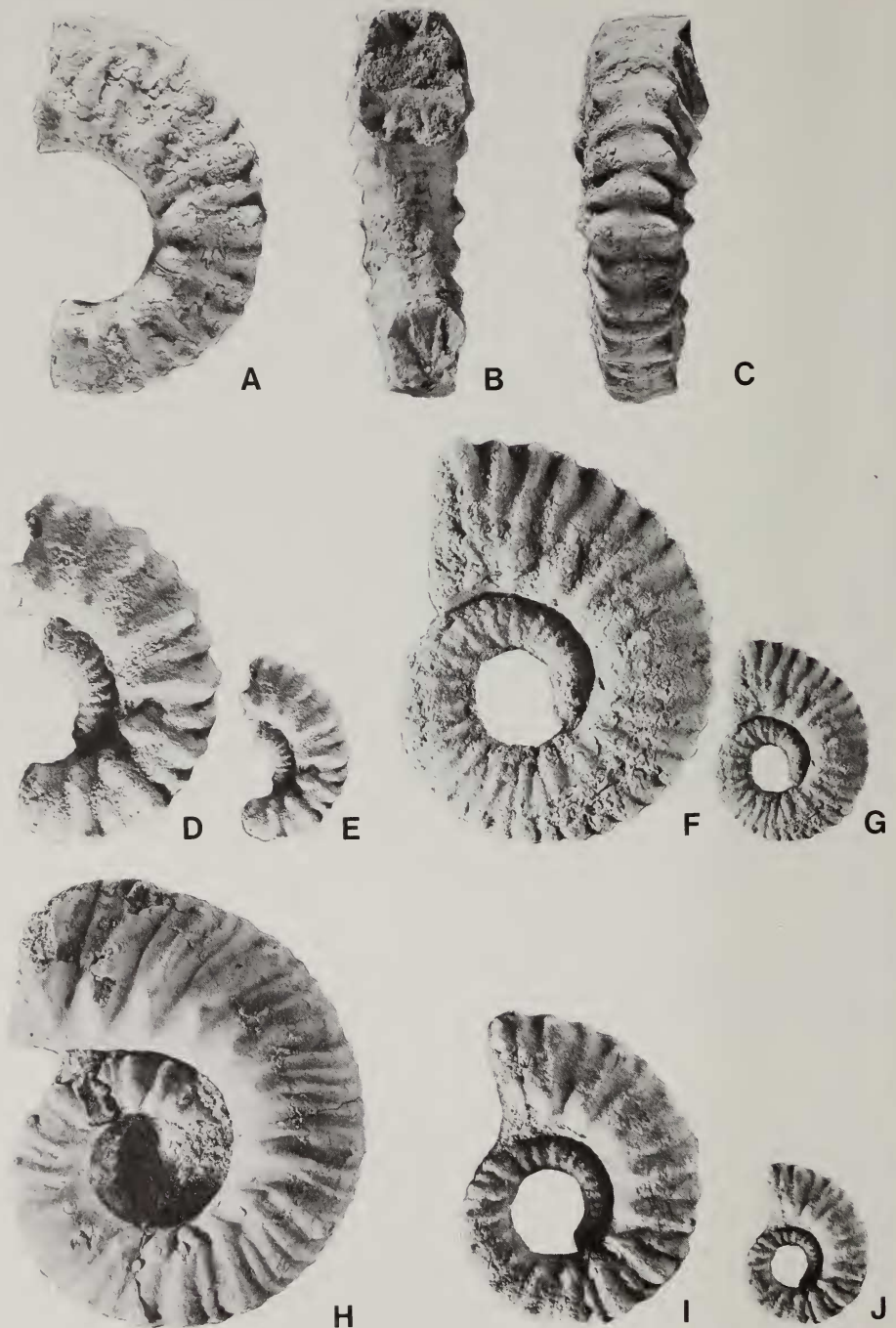


Fig. 17. *Myloceras bituberculatum* sp. nov. A-C. SAM-PCZ7301. D-E. SAM-PCZ8331. D. $\times 2$, E. $\times 1$. F-G. SAM-PCZ8332. F. $\times 2$, G. $\times 1$. H. SAM-PCZ7299a, holotype. $\times 1$. I-J. SAM-PCZ8333. I. $\times 2$, J. $\times 1$.

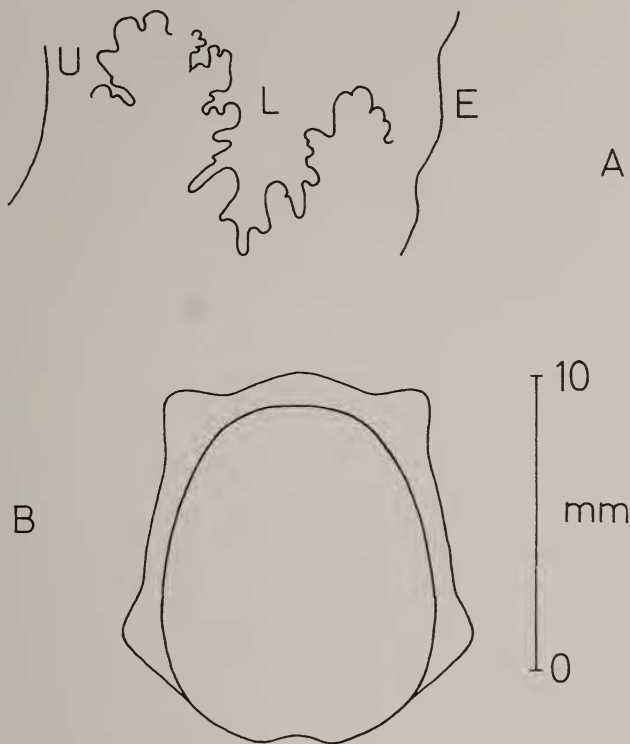


Fig. 18. *Myloceras bituberculatum* sp. nov. A. Suture line of SAM-PCZ7301. B. Whorl section of SAM-PCZ7301. Scale bar to size for A and B.

slightly with growth, in the available material ranging from 36 to 41 per cent of the diameter.

The whorl section is trapezoidal, higher than wide to very compressed, with a narrower venter than dorsum. The flanks are virtually flat (Fig. 18B).

Ornament is very robust, consisting of prominent umbilical tubercles, bifurcating and intercalated ribbing and ventral tubercles. The umbilical tubercles are situated on the outer edge of the umbilical wall, and are conical to radially elongated. From these a prorsiradiate, slightly sinusoidal pair of ribs generally arises. In addition, intercalatory ribs may arise at the umbilical edge or up to a midflank position. On the early whorls of some specimens single ribs, arising at the umbilical tubercles, alternate with intercalatory ribs arising at midflank.

Ventral tuberculation is variable, both within the same or between different specimens. All ribs may bear a pair of distinctly clavate tubercles or major ribs, with prominent clavate tubercles, may alternate with weaker ribs, either without tuberculation at all, or only with weak, conical ventral tubercles. All ribs cross the venter with a slight forward curvature and broadening.

The suture line is only partially exposed in PCZ7301 (Fig. 18A).

Dimensions

<i>Specimen number</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
PCZ7299a	62	19 (30,6)	21 (33,8)	0,90	24 (33,8)
PCZ7299b	61	16 (26,2)	21 (34,4)	0,76	25 (41)
PCZ7300	—	18 (1)	23 (—)	0,78	—
PCZ7301	51	15 (29,4)	18 (35,3)	0,83	21 (41,2)
PCZ7302	36	10 (27,8)	15 (41,7)	0,67	13 (36,1)
PCZ7303	—	12 (—)	16 (—)	0,75	—
PCZ7304	24	7 (29,2)	9 (37,5)	0,78	9 (37,5)
PCZ8332	26	6 (23,0)	10 (38,5)	0,60	10 (38,5)
PCZ8333	21	5,5 (20,2)	8 (38,1)	0,69	8,5 (40,5)

Discussion

This species and *M. paradoxus* (Collignon, 1964) (see Kennedy 1985: 307–309, figs 11–12) are unique amongst *Myloceras* in possessing distinct umbilical tubercles. *Myloceras bituberculatum* differs from *M. paradoxus* in having much stronger and wider-spaced ribbing. As far as whorl section and frequency of ribbing on the venter are concerned, affinities may be sought with *M. besairiei* Collignon and *M. robustum* Klinger, but the presence of umbilical tubercles clearly distinguishes the present material.

Förster (1975: 185) described part of a crozier with incipient umbilical tubercles from Mozambique as *M. cornucopium*. This fragment has a whorl-section that is wider than high, and I doubt if it can be referred to the present species.

Due to the imprecise locality data I do not know what—if at all, the accompanying *Labeceras* dimorph is.

Occurrence

Upper Albian of Zululand.

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* Note added at proof stage (see p. 204).

New material has been described from Patagonia (Aguirre Urreta, M. B. & Riccardi, A. C. 1988. Albian heteromorph ammonoids from southern Patagonia, Argentina. *Journal of Paleontology* **62** (4): 598–164). This includes *Labeceras crassetuberculatum* Klinger *magnum* ssp. nov., *L. singulare* (Leanza, 1970) and *Myloceras (Calliscaphites) andinus* Leanza. *Calliscaphites* is retained as a subgenus of *Myloceras* on account of its alleged crioceratitid coiling. Judging by the compressed whorl section and regular ornament of the type and only species, *M. (C.) andinus*, it appears to be close to the group of *M. besairiei* and '*Ellipsoceras expansum*'. On the whole, description of this fauna does not change any of the opinions expressed in this article.